The Journal of Research on the Lepidoptera

Volume 45: 39-47

THE LEPIDOPTERA RESEARCH FOUNDATION, 19 April 2012

ISSN 0022-4324 (print)
ISSN 2156-5457 (online)

On the taxonomic status of *Tirumala tumanana* Semper, 1886 (Lepidoptera: Nymphalidae, Danainae)

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Abstract. Based on new information gathered from Scanning Electron Microscopy of the male alar and abdominal androconial organs, together with wing pattern and male genitalia characters, the nominal species *Tirumala tumanana* Semper, 1886, is demonstrated to be a distinct and geographically isolated species of *Tirumala* from extreme southern Philippines. For more than a century this taxon has been placed as a subspecies of *T. choaspes* (Butler, 1866) or of *T. limniace* (Cramer, 1775). The androconial organ data demonstrate that *T. tumanana* belongs to the *limniace* species group, and is not closely related to *T. choaspes*.

Key words: Lepidoptera, Nymphalidae, Danainae, *Tirumala*, species status, androconial organs, body size, *Tirumala tumanana*, *T. limniace*, *T. choaspes*, Philippines.

Introduction

Semper (1886) described what he considered to be a new species of milkweed butterfly from Tumanao, southern Philippines, as *Tirumala tumanana*. At that period Semper was still working in the taxonomic tradition that gave specific status to taxa from adjacent regions and islands if they presented discrete, even if small differences in color pattern. Soon after, however, systematists such as Karl Jordan working with Walter Rothschild introduced the polytypic species concept and with it, the advent of trinominal nomenclature (Mallet, 2004). By the time 'Seitz' started to appear some 20–25 years later, most butterfly workers had embraced the subspecies approach. As a result, despite continuing discovery of new regional and island forms, in groups such as the Danainae the number of full species recognized began to fall (Ackery & Vane-Wright, 1984: text-fig. 1).

Received: 26 October 2011
Accepted: 1 March 2012

In his description of *Tirumala tumanana*, Semper stated that it was most similar in appearance to *T. choaspes* (Butler, 1866) from Sulawesi, but he also compared it structurally with *T. orientalis* (Semper, 1879) from the Philippines. Today *orientalis* is treated as a subspecies of the widespread and highly polytypic *T. hamata* (Macleay, 1827).

Despite the outstanding appearance of *T. tumanana* ("it forms a very distinctive race": Ackery & Vane-Wright, 1984: 44), given the dominance of the polytypic species concept in butterfly classification, it is not surprising that throughout most of the 20th century Semper's *tumanana* was treated as a subspecies—either of *T. choaspes*, as presaged by Semper (1886), dealt with by Fruhstorfer (1910), Talbot (1943) and others, and followed by Ackery & Vane-Wright (1984)—or of *T. limniace* (Cramer, 1775), as proposed with good arguments by Morishita (1981: 461) and followed by Treadaway (1995). Despite this, Morishita (1981), Ackery & Vane-Wright (1984) and Vane-Wright & de Jong (2003) all also expressed the view that *tumanana* probably deserved specific rank. Most recently, based on male genitalia and wing pattern characters, Treadaway & Schroeder (2012) have returned it to full species status. The purpose of the paper is to assess this proposal in the light of new evidence from the androconial organs, together with the genitalia and wing pattern characters.

Synonymy and type material

Tirumala tumanana Semper, 1886

Tirumala tumanana Semper, 1886: 15. PHILIPPINES: Lectotype male, Sarangani Is., Tumanao. Senckenberg Museum, Frankfurt a. M. [examined HGS & CGT], here designated (see below).

Danaida (*Tirumala*) *choaspes* "Lokalform"; Fruhstorfer, 1910: 205.

Danaida (*Tirumala*) *choaspes* in part; Hulstaert, 1931: 49.

Tirumala choaspes tumanana; Bryk, 1937: 107.

Danaus choaspes Butler, in part; Talbot, 1943: 137.

Tirumala limniace tumanana; Morishita, 1981: 460–462, pl. 94 (3 figs.: ♂ ♀), and 2008: 3; Treadaway, 1995: 62.

Tirumala choaspes tumanana; D'Abrera, 1982: 206; Ackery & Vane-Wright, 1984: 44, 130, 198, pl. VII fig. 55.

Tirumala tumanana [distinct species?]; Vane-Wright & de Jong, 2003: 218.

Tirumala tumanana; Treadaway & Schroeder, 2012: 29, 55.

Tirumala tumanana was described by Georg Semper from two male specimens. Both represent, without doubt, the same taxon. One of these syntypes, labelled Sarangani Is., Tumanao, 24. vi. 1882, forewing length (fwl hereafter) 43 mm, is hereby designated lectotype of the nominal taxon *Tirumala tumanana* Semper, 1886, and has been labelled accordingly. The second syntype, with identical data but also labelled Gen.-Praep. 477 I. Schroeder, with fwl 47 mm, has been labelled paralectotype. Both specimens are in the Lepidoptera collection of the Senckenberg Museum, Frankfurt am Main.

Characters

Alar organs (Fig. 1). Butterflies of the subtribes Amaurina and Danaina produce pheromone transfer particles (PTPs hereafter) in several different ways (Brower *et al.*, 2010). Those of *Tirumala* are outstanding, as in all species of the genus they are produced by fragmentation of cushion scales formed within the pouched hindwing alar organs (Boppré & Vane-Wright, 1989). Hashimoto & Yata (2007, 2008a) carried out a systematic survey of the genus, using SEM, and found that, among the Asian species, the PTPs of *T. gautama* (Moore, 1877), *choaspes*, *ishmoides* Moore, 1883, *septentrionis* (Butler, 1874), *hamata* and *euploeomorpha* (Howarth, Kawazoé & Sibatani, 1976) are all roughly rounded in form. Although each species appears to differ slightly in shape, they can all be considered similar to each other. In contrast, those of *T. limniace* and its putative sister species, the African *T. petiverana* (Doubleday, 1847) are distinctly polyhedral, not rounded. KH has now produced SEMs of *T. tumanana*, and its PTPs are polyhedral, very similar to *limniace* but not to *choaspes* (Fig. 1; cf. Hashimoto & Yata, 2007: figs. 8–10). The PTPs of

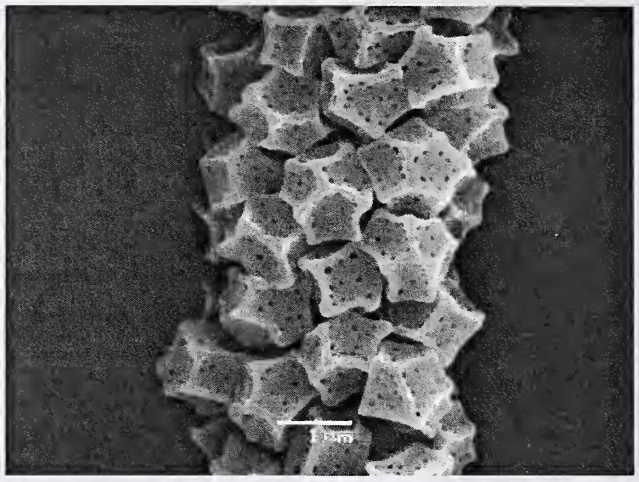

Figure 1. *Tirumala tumanana*. Short section of cushion scale within male alar organ, showing numerous, *limniace*-like polyhedral PTPs still attached (specimen in Osada Collection, Japan). Scale bar: 1 µm. SEM by Kei Hashimoto.

T. choaspes are wrinkled, and in this respect similar to those of *T. gautama* (Hashimoto & Yata, 2008a: figs. 1a,b). The PTPs of the exclusively African clade represented by the polytypic species *T. formosa* (Godman, 1880) are very distinct (Boppré, 1976; Boppré & Fecher, 1977; Hashimoto & Yata, 2008a: fig. 2).

Abdominal hairpencils (Figs. 2, 3). The abdominal hairpencils of *Tirumala* are also unique among Amaurina and Danaina: they do not produce PTPs, and comprise only the one hair type, 'particle receiving hairs' (Boppré & Vane-Wright, 1989: 117). Hashimoto & Yata (in prep.) have now studied the microstructure of the receiving hairs in representatives of all currently recognised species of *Tirumala* except *T. alba* Chou & Gu, 1994 (see Discussion). Their results indicate that differences observable over the distal 40% of the length of the hairs can be used to group the species in the same way as the PTPs: (*petiverana* + *limniace*), (*gautama* + *choaspes*), (*septentrionis* + *ishmoides* + *hamata* + *euploeomorpha*), with *formosa* again unique. *T. petiverana* and *T. limniace* have what can be described as 'dense granular processes', and this pattern is also seen in *T. tumanana* (Figs. 2, 3). In contrast, the surface ornamentation of the median-distal area of the hairs of *T. gautama* and *T. choaspes* has the crest processes very prominent, presenting a very different appearance. Species belonging to the *hamata* group exhibit ladder-like swirling patterns without dense granules, while *T. formosa* has very coarse grains (Hashimoto & Yata, unpubl. observations).

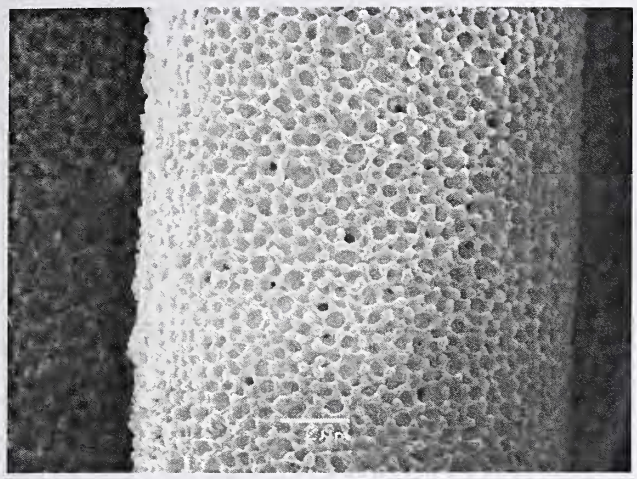

Figure 2. *Tirumala tumanana.* Short section of hair of male abdominal organ showing surface sculpture (specimen in Osada Collection, Japan). Scale bar: 2 µm. SEM by Kei Hashimoto.

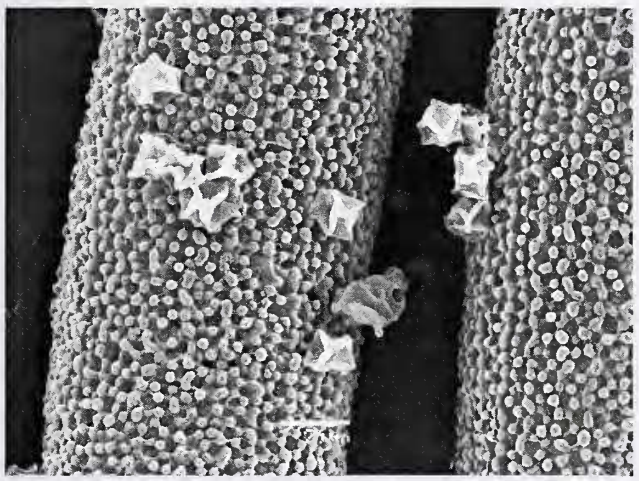

Figure 3. *Tirumala tumanana.* Short sections of abdominal organ hairs, with PTPs from the alar organ attached (specimen in Morishita Collection, Japan). Scale bar: 2 µm. SEM by Kei Hashimoto.

Male genitalia (Figs. 4, 5). As demonstrated by Morishita (1981) and Ackery & Vane-Wright (1984), the highly asymmetrical phalli of *Tirumala* do offer characters that are useful for species separation. Phalli of all *Tirumala* species except *T. alba* (see Discussion) and *T. tumanana* have been illustrated by Hashimoto & Yata (2008b: 16). KH has recently had the opportunity to examine the genitalia of *tumanana*, and her drawings are presented as Fig. 4a, together with her earlier drawings of the phallus of *T. limniace* for comparison (Fig. 4b).

Working independently, HS and CGT have also examined the phalli of *T. tumanana* and *T. limniace*. HS notes the most obvious difference between them: in *limniace* the almost right-angled offset apex gives the effect of being inflated; the phallus it is also set with numerous microtrichia (Fig. 5b). In *tumanana* the phallus from the base to apex is equally wide in dorsal aspect, flatly curved subapically, and has a linear series of thorn-like processes (Fig. 5a).

Wing pattern (Figs. 6, 7). With respect to the wing pattern of *Tirumala tumanana*, Morishita (1981) noted that the "prominent subapical band composed of three bluish white spots [in forewing cells R_5, M_1, M_2] is a quite unique pattern otherwise not found in this genus" (Fig. 6). The three large spots in cells R_5, M_1, M_2 are submarginals, and far larger than the postdiscal spots located at the bases of these cells, these particular postdicals in *tumanana* being almost obsolete. In contrast, *T. limniace* has the corresponding postdiscals well-marked, and usually far larger than the submarginals in the same cells (Fig. 7). Like *T. choaspes* but unlike *T. limniace*, *T. tumanana* lacks an outer postdiscal pale spot in forewing cell CuA_2 between the large basal pale marking and the small submarginal and marginal pale spots (Fig. 6). The underside melanic pattern of *T. tumanana* is very dark, almost black and almost as dark as the upperside, unlike most *T. limniace* in which the underside usually appears considerably paler than the upperside (Figs. 6, 7). Overall, the pattern of both sexes of *T. tumanana*, although so like other *Tirumala* in many respects, is instantly recognisable. In comparison to all subspecies of *T. limniace*, wing pattern alone could be considered justification for reinstating *T. tumanana* to species rank.

Adult size. ♂ forewing length 44.08 mm (mean of 17 specimens from South Cotabato: 15 from the Treadaway Collection, 2 from same source deposited in BMNH; observed range 36.8–47.0 mm; SD = 2.54 mm; 1 ♂ from Balut Island: 43 mm; 3 ♂ from Sarangani Island: 45 mm, 43 mm (lectotype), 45 mm (paralectotype).

♀ forewing length 45.38 mm (mean of 17 specimens from South Cotabato: 11 in Treadaway Collection, 6 from same source in BMNH; observed range 40.0–51.0 mm; SD = 2.78 mm; 1 ♀ from Balut Island: 42.5 mm.

With respect to the 17 males and 17 females from South Cotabato, although females have a mean forewing length 1.3 mm greater than the males, the difference based on these data is not statistically significant (two-sided *t*-test, unknown variances assumed equal: $t_{32df} = 1.423$, $p > 0.1$).

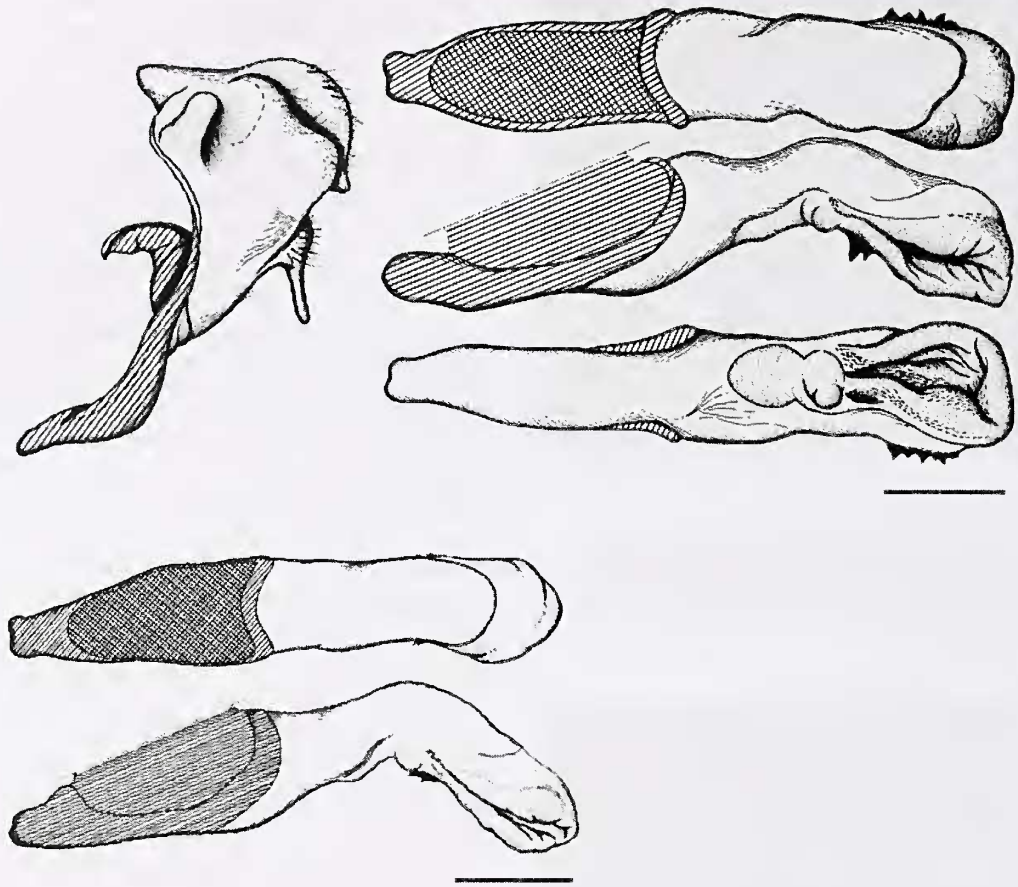

Figure 4. Male genitalia of *Tirumala*. **4a** (above) — *T. tumanana* (Sarangani Island, 3.i.1980, Osada Collection); left: with phallus removed, lateral view; right: dorsal (upper), lateral (middle) and ventral (lower) views of the phallus (KH del.). **4b** (below) — *T. limniace limniace*, phallus (Hainan); dorsal (upper) and lateral (lower) views (from Hashimoto & Yata, 2008b: fig. 11E). Scale bars (phallus): 1 mm.

Distribution and bionomics

Distribution (Figs. 8, 9). *Tirumala tumanana* is only known to occur on the major island of Mindanao (Republic of the Philippines), and two small islands, Balut and Sarangani, situated immediately off its southernmost point (Figs. 8, 9). Old records for "Manila" (e.g. Adams and Rothschild collections, in BMNH) are certainly erroneous. Tumanao is the name of a small harbour on Sarangani, and the stream that flows into it. Until now all records for the main island were from the extreme south, in the provinces of South Cotabato and Davao del Sur. However, the discovery of two old specimens from Dapitan, in the north-eastern part of the island (Fig. 9), although these records must be questioned, raises the possibility that this species was once more widespread on Mindanao (see Discussion).

Known localities: Philippines, Mindanao. Zamboanga Peninsula, Zamboanga de Norte: Dapitan (two males in National Museum of Wales labelled "Dapatan"). South Cotabato: T'boli (Lake Maughan, Mt. Parker; Siman; Mt. Busa; Mt. Matutum), and Lake Sebu. Davao del Sur: Sarangani Island (Tumanao), and Balut Island. Recorded at altitudes from 350–1900 m, during April–June and August–December.

Mindanao appears to be a genuine gap in the distribution of *T. limniace*, filled only in part by *T. tumanana* if this taxon is seen as its vicariant. *T. limniace* is also absent from Sumatra, eastern Borneo (Morishita, 1981), the Sangihe and Talaud archipelagos and northern Sulawesi (Vane-Wright & de Jong, 2003), and North and Central Maluku (Ackery & Vane-Wright, 1984). Moreover, it is very rare in the Malay Peninsula and its supposed presence in Sarawak has never been confirmed (Ackery & Vane-Wright, 1984). Thus, with respect to *limniace*, *T. tumanana* is completely isolated (Fig. 8). There

Figure 5. Phalluses of *Tirumala*. **5a** (above) — *T. tumanana*. **5b** (below) — *T. limniace*. Scale bar: 1 mm. (Light micrographs by Inge Schroeder, Senckenberg Museum.)

are no other records to confirm Dapitan, and it may be that this species, at least now, is entirely restricted to the Sarangani Islands and the mountainous areas of southern Mindanao just west of Sarangani Bay (Fig. 9).

Life history. The life history and larval foodplants of *Tirumala tumanana* are unknown. Fukuda & Lee (2009), who provided numerous excellent images of the early stages of *T. limniace*, found that on Taiwan *limniace* was monophagous on *Dregea volubilis* (Apocynaceae: Asclepiadoideae). In addition to *Dregea*, Ackery & Vane-Wright (1984: 199) recorded five other asclepiad genera as hosts: *Asclepias*, *Calotropis*, *Heterostemma*, *Hoya* and *Marsdenia*, together with *Crotalaria* (Fabaceae) and *Cocculus* (Menispermaceae), while Robinson *et al.* (2001) noted additional records for *Holarrhena* (Apocynaceae: Apocynoideae), *Tylophora* (Asclepiadoideae) and even *Saccharum* (Poacaeae). Given the state of taxonomy of the Apocynaceae, and the problem of misidentifications of both butterflies and hostplants, most of these records must be viewed with caution (see discussion in Brower *et al.*, 2010). Fukuda & Lee (2009) noted that, in Japan, female *T. limniace* would not oviposit on *Cynanchum japonicum*, *Marsdenia tinctoria* var. *tomentosa*, *Heterostemma brownii*, *Tylophora tanakae* (Asclepiadoideae) or *Parsonsia* (Apocynoideae), while they would lay eggs on *Marsdenia tomentosa* and *Hoya carnosa*—but much preferred *Dregea volubilis*. Fukuda & Lee (2009) also give a list of 13 plants which, in Japan, *T. limniacae* larvae will not eat, including *Hoya carnosa*, *Marsdenia tinctoria* var. *tomentosa*, *Tylophora tanakae*, *T. ovata* and *Asclepias curassavica*. All non-dogbane family records are highly improbable (Fukuda & Lee, 2009: 53). The most likely hostplants of *T. tumanana* will be found to belong to one or more species of Asclepiadoideae endemic to Mindanao.

Discussion

During a brief visit to the National Museum of Wales, Cardiff, in November 2010, one of us (RIVW) came across two very old male specimens of *Tirumala tumanana* from the Rippon Collection, labelled "Dapatan" [= Dapitan, Mindanao]. The ultimate origin of this material is unknown, but Kirk-Spriggs (1995) lists H. Cuming (1791–1865), F.J.S. Parry (1810–1885) and C.G. Semper (1832–1893) as sources of Philippine material in Rippon's collection. Dapitan, a medium-sized coastal town on the northern Zamboanga Peninsula, represents a significant extension of the known range of *T. tumanana* on Mindanao. While this must be questioned, at present there is no obvious reason to reject this historical record. Talbot (1943: 137) notes a specimen of *Tirumala ishmoides* from Dapitan, so this is a known butterfly locality.

This discovery reminded RIVW of the status question affecting this taxon. He contacted Osamu Yata and KH in Japan, and CGT in Germany, to see if they were interested in addressing it. Subject to availability of material (subsequently obtained on loan), KH indicated she would be willing to undertake scanning electron micrography of the androconia, and dissections of male genitalia. CGT replied that, in collaboration with HGS, he was finalising a new catalogue of Philippine butterflies (Treadaway & Schroeder, 2012). In this work, based on wing pattern and male genitalia, they proposed to reinstate *T. tumanana* as a species close to but distinct from *T. limniace*, and not closely related to *T. choaspes*.

Our combined investigations fully endorse this last view. As described above, based on microstructure, the alar and abdominal androconial organs of *T. tumanana* are almost inseparable from those of *T. limniace*, with those of the latter being significantly different from *T. choaspes* and *T. hamata* (Hashimoto & Yata, 2007, 2008a, and unpublished observations). This then leaves only two possibilities: either *tumanana* is a subspecies of *limniace*, as Morishita (1981) proposed, or it is a species in its own right. As the two taxa are not known to co-occur, there is inevitably some degree of subjectivity in deciding on taxonomic rank.

Given the striking difference between the phalli of the two taxa (*tumanana* compared with several subspecies of *limniace*), and the unique and immediately recognizable wing pattern of both sexes of *tumanana*,

Figure 6. *Tirumala tumanana*, adult male, Sarangani Island, 3.i.1980 (Y. Osada) (Kitakyushu Museum). Left: upperside; right: underside. Forewing length: 50 mm. (Photographs: Kei Hashimoto.)

Figure 7. *Tirumala limniace limniace*, adult male, India, Khasi Hills (M. Nakayama Collection). Left: upperside; right: underside. Forewing length: 51 mm. (Photographs: Kei Hashimoto.)

we believe that the most appropriate status for *T. tumanana* is that of a distinct species in its own right, as proposed by Treadaway & Schroeder (2012).

T. tumanana therefore joins the small group of *Tirumala* species with restricted ranges—the others being *T. alba* known only from Hainan, and *T. euploeomorpha* from the easternmost islands of the main Solomons archipelago (Tennent, 2002). The latter has been confirmed as a member of the *hamata* group by Hashimoto & Yata (2008a), and the possibility remains that *euploeomorpha* is a vicariant, mimetic subspecies of *T. hamata* (see also discussion in Tennent, 2002: 112). *T. alba* also requires further investigation, being the only currently recognised species of *Tirumala* yet to have its androconia studied in detail. Described from a unique specimen (Chou, 1994: 275, 755), it seems possible that *T. alba* is merely an albinotic aberration of *T. limniace limniace*, a species well-known from Hainan. Given these possibilities, the existence of *T. tumanana* as a distinct species narrowly endemic to the far southern Philippines is all the more remarkable.

Finally, a brief comment on adult size is called for. It is generally accepted that in most butterfly species

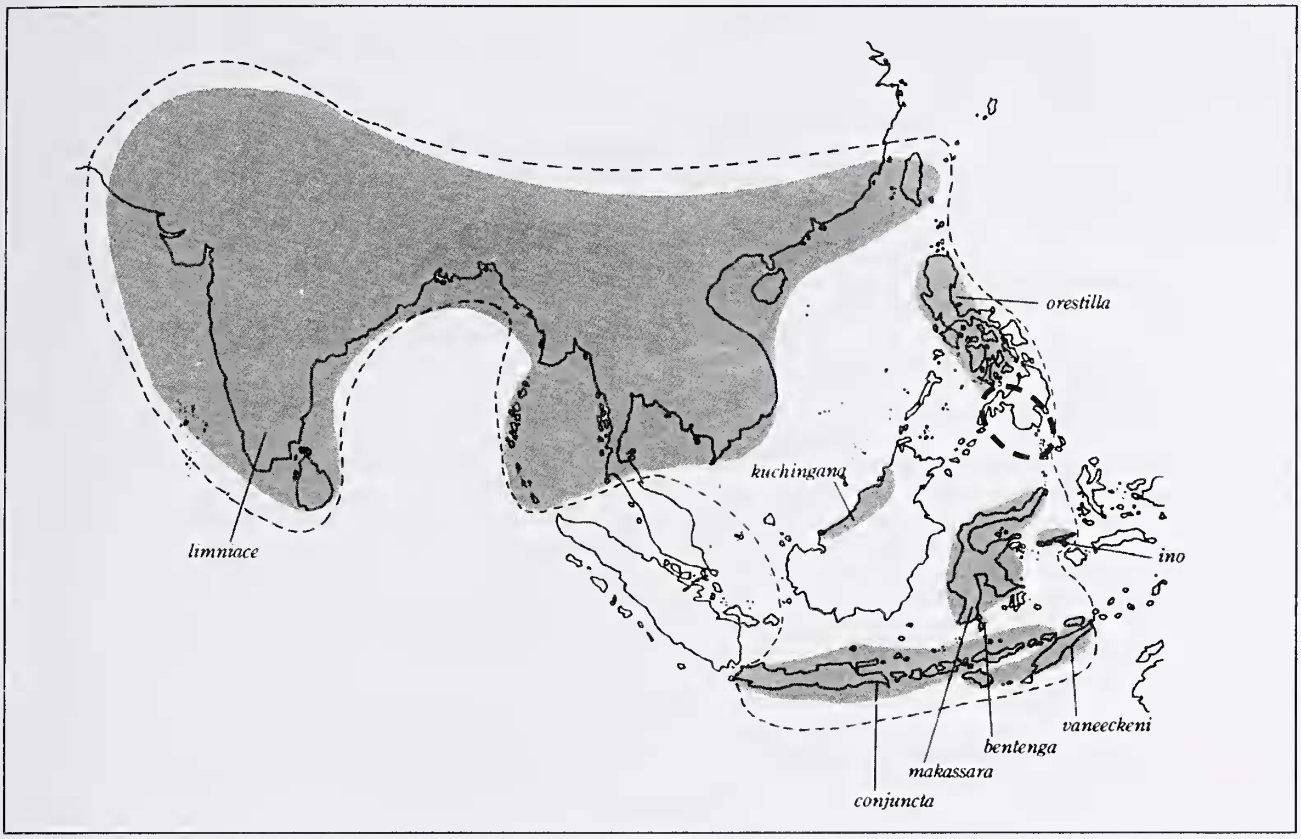

Figure 8. Distribution map of *Tirumala limniace*, which occurs as a series of subspecies from Afghanistan and Sri Lanka east to the northern and central Philippines, Sula Archipelago and Timor. Note the disjunctions, with 'gaps' in Borneo (where the presence of *T. l. kuchingana* (Moulton, 1915) has never been confirmed), Palawan, Sumatra, northern Sulawesi (not as shown here: see Vane-Wright & de Jong, 2003) and Mindanao. The species does occur rarely in the Malay Peninsula. Southern Mindanao is occupied by *T. tumanana* (pecked oval; for details see Fig. 9). Map modified from Morishita (1981: 460) with permission.

females are, on average, "larger" than males—as reflected by weight on eclosion (rarely measured) or forewing length (widely used as a 'standard' measure of butterfly size). There are exceptions, however, as recently documented for example by Liseki & Vane-Wright (2011) for two swallowtail species from Tanzania, in which the males undoubtedly have greater forewing mean lengths than their females.

This suggests the strong possibility that the sexes of some butterfly species may not differ in mean size, at least as measured by forewing length—or that if they do but the differences are small, this may only be detectable from large samples. Size is an important life-history trait that interacts with, for example, fecundity, longevity, and flight activity (Gilchrist, 1990). In Danainae it may be significant that males are particularly active in foraging for pyrrolizidine alkaloids (Brower *et al.*, 2010) and, when copulating pairs are disturbed, the male is the active partner in flight (Miller & Clench, 1968). To the best of our knowledge sexual dimorphism in size has never been systematically investigated in the Danainae. The result obtained here that, on available data, male and female *Tirumala tumanana* are not significantly different in size, points to the need for systematic studies on size dimorphism in butterflies generally, and Danainae in particular.

Acknowledgements

KH wishes to thank Kyoichiro Ueda (Kitakyushu Museum of Natural History and Human History) for the loan of material collected by the late Yasunobu (Shilo) Osada, Kazuhiko Morishita for loan of material from his own collection, and Osamu Yata, Toyokazu Yoshida and Yasusuke Nishiyama for much assistance. RIVW wishes to acknowledge the kind help of Brian Levey (National Museum of Wales, Cardiff), and Clive Moncrieff for advice on statistics. The authors are grateful to Konrad Fiedler for

Figure 9. Map of Philippines, with well-established localities for *Tirumala tumanana* plotted as diamonds (those for the two small Sarangani Islands, Balut and Sarangani, offset). The single circular symbol indicates the general location of Dapitan, where the butterfly may also have occurred in the past (see text).

constructive criticism of the first draft. Finally, we are most grateful to Dr Morishita for kind permission to base Fig. 8 on his work.

Literature cited

Ackery, P.R. & R.I. Vane-Wright. 1984. Milkweed butterflies: their cladistics and biology. New York, Cornell University Press. ix + 425 pp.

Boppré, M. 1976. Pheromon-Transfer-Partikel auf einem Duftpinselhaar eines Monarchfalters (*Danaus formosa*). Naturwissenschaftliche Rundschau, Stuttgart 29(9): [caption to frontispiece].

Boppré, M. & K. Fecher. 1977. Structural complexity of scent organs of male danaid butterflies. Scanning Electron Microscopy, IIT Research Institute, Chicago 2: 630, 639–644.

Boppré, M. & R.I. Vane-Wright. 1989. Androconial systems in Danainae (Lepidoptera): functional morphology of *Amauris*, *Tirumala*, *Danaus* and *Euploea*. Zoological Journal of the Linnean Society 97: 101–133.

Brower, A.V.Z., N. Wahlberg, J.R. Ogawa, M. Boppré & R.I. Vane-Wright. 2010. Phylogenetic relationships among genera of danaine butterflies (Lepidoptera: Nymphalidae) as implied by morphology and DNA sequences. Systematics and Biodiversity 8: 75–89.

Bryk, F. 1937. Danaidae I, II, 702 pp. *In*: F. Bryk (editor), Lepidopterorum Catalogus 28(78,80). 's-Gravenhage, W. Junk.

Chou, I. (ed.) 1994. Monographia Rhopalocerorum Sinensium (two

volumes). Henan (China), Henan Scientific and Technological Publishing House. [vii] + 1–408; [i] + pp. 409–854 pp.

D'Abrera, B. 1982. Butterflies of the Oriental Region. Part 1. Papilionidae, Pieridae & Danaidae. Ferny Creek, Victoria (Australia), Hill House. xxi + 244 pp.

Fruhstorfer, H. 1910–1911. Danaidae, pp. 191–284, 13 pls. *In*: A. Seitz (editor), Gross-Schmetterlinge der Erde (2)9. Stuttgart, Fritz Lehmann.

Fukuda, H. & H-T. Lee. 2009. Life histories of *Tirumala limniace* and *T. septentrionis* (Nymphalidae, Danainae) in Taiwan with special reference to their overwintering stages, larval foodplants, and immature stages. Butterflies (52): 40–54.

Gilchrist, G.W. 1990. The consequences of sexual dimorphism in body size for butterfly flight and thermoregulation. Functional Ecology 4: 475–487.

Hashimoto, K. & O. Yata. 2007. Comparison of microstructure of pheromone transfer particles (PTPs) in the genus Tirumala (Lepidoptera, Nymphalidae, Danainae). Transactions of the Lepidopterological Society of Japan 58: 177–182.

Hashimoto, K. & O. Yata. 2008a. Comparative morphological study in the genus *Tirumala* (Lepidoptera, Nymphalidae, Danainae): sexual isolation and PTPs. Transactions of the Lepidopterological Society of Japan 59: 305–311.

Hashimoto, K. & O. Yata. 2008b. A comparative morphological study of the genus *Tirumala* based on the male genitalia (Lepidoptera, Nymphalidae, Danainae). Butterflies (Teinopalpus) (50): 13–18.

Hulstaert, R.P.G. 1931. Lepidoptera Rhopalocera: Fam. Danaididae: Subfam. Danaidinae & Tellervinae, 215 pp., 6 pls. *In*: P. Wytsman (editor), Genera Insectorum 193. Bruxelles, Verteneuil & Desmet.

Kirk-Spriggs, A.H. 1995. Robert Henry Fernando Rippon (ca 1836–1917), naturalist and zoological illustrator. Archives of Natural History 22: 97–118.

Liseki, S.D. & R.I. Vane-Wright. 2011. Butterflies (Lepidoptera: Papilionoidea) of Mount Kilimanjaro: introduction and family Papilionidae. Journal of Natural History 45: 2375–2396.

Mallet, J. 2004. Poulton, Wallace and Jordan: how discoveries in *Papilio* butterflies led to a new species concept 100 years ago. Systematics and Biodiversity 1: 441–452.

Miller, L.D. & H.K. Clench. 1968. Some aspects of mating behavior in butterflies. Journal of the Lepidopterists' Society 22: 125–132.

Morishita, K. 1981. Danaidae, pp. 123–204 (pls 85–162), 439–598 (text). *In*: E. Tsukada (editor), Butterflies of the South East Asian Islands 2. Tokyo, Plapac. [In Japanese; also consulted in English translation, 1985.]

Morishita, K. 2008. A survey of the Danainae and Tellervinae (Lep. Nymphalidae). The Nature & Insects 43: 2–5, 2 pls. [in Japanese]

Robinson, G.S., P.R. Ackery, I.J. Kitching, G.W. Beccaloni & L.M. Hernández. 2001. Hostplants of the moth and butterfly caterpillars of the Oriental region. Kuala Lumpur, Southdene & London, NHM. 744 pp.

Semper, G. 1886–1892. Die Tagfalter: Rhopalocera. Die Schmetterlinge der Philippinischen Inseln: Beitrag zur Indo-Malayischen Lepidopteren-Fauna. Wiesbaden, C.W. Kreidel. 1: xiv + 380 pp., 2 + 49 pls.

Talbot, G. 1943. Revisional notes on the genus *Danaus* Kluk (Lep. Rhop. Danaidae). Transactions of the Royal Entomological Society of London 93: 115–148.

Tennent, J. 2002. Butterflies of the Solomon Islands. Dereham (UK), Storm Entomological Publications. xxiv + 413 pp.

Treadaway, C.G. 1995. Checklist of the butterflies of the Philippine Islands (Lepidoptera: Rhopalocera). Nachrichten des entomologischen Vereins Apollo Frankfurt, Suppl. 14: 7–118.

Treadaway, C.G. & H.G. Schroeder. 2012. Revised checklist of the butterflies of the Philippine Islands (Lepidoptera: Rhopalocera). Nachrichten des entomologischen Vereins Apollo Frankfurt 32, Suppl. 20: 1–64.

Vane-Wright, R.I. & R. de Jong, R. 2003. The butterflies of Sulawesi: annotated checklist for a critical island fauna. Zoologische Verhandelingen Leiden (343): 1–267.